

A NEW ZOSTEROPHYLL FROM THE LOWER DEVONIAN OF POLAND

by DANUTA ZDEBSKA

ABSTRACT. A new genus and species *Konioria andrychoviensis* assigned to the Zosterophyllophytina is described from the Lower Devonian (Emsian) of two boreholes in the Bielsko-Andrychów area of the Polish Western Carpathians. *K. andrychoviensis* possesses dichotomous axes covered on their lower part with long subulate spines and on their upper part with short triangular spines. Apices of axes form hooks. In addition to spines, the axes show 1-4 longitudinal wings. The reniform to rounded sporangia are borne singly at dichotomies. The structure of pyritized axes shows a central exarch strand with scalariform tracheids and a hypodermis. In connection with the unusual position of the sporangia the problem of the evolution of the lycopod sporophyll is discussed. *Konioria* appears to suggest that the lycopod sporophyll originated from ends of fertile axes, in accordance with the Telome Theory of Zimmermann (1930). The Telome Theory, however, is based on the *Rhynia*-type of organization, while other evidence suggests that the lycopods originated from the Zosterophyllophytina.

THIS paper describes a single species obtained from two bore-holes, Andrychów 2 and Andrychów 4 in the Bielsko-Andrychów area of the Polish Western Carpathians (see Turnau 1974). The depth in Andrychów 2 is between 2300.8 and 2306.6 m and in Andrychów 4 between 2245.5 and 2250.8 m. The age of these rocks was determined as Lower Devonian (Emsian) on the basis of their lithology by Konior (1965, 1966, 1968, 1969) and this was confirmed by the miospores (Konior and Turnau 1973; Turnau 1974).

Fragments of *Drepanophycus spinaeformis* Goepp. and *Dawsonites* sp. have been recovered from the same cores, but have still to be described. Preliminary investigations of the plant material were carried out by Maria Reymanówna who gave a short description of *Konioria* under the name of *Psilophyton* sp. referred to in Konior (1965). Well-preserved fragments of the plant allow conclusions to be drawn on its systematic position and on the probable course of evolution of the lycopod sporophyll.

MATERIAL AND METHODS

The plant axes are preserved as coaly compressions in a dark-grey siltstone. These remain intact when removed from the matrix with hydrofluoric acid. When macerated in Schulze's solution, most disintegrated and showed no cells. Several axes yielded tracheid fragments with circular bordered pits. A few cuticle fragments of axes are in a state of natural maceration. These are translucent enough to show both a central dark vascular strand and stomata. Certain other axes were pyritized and were not very compressed. From these, thin sections were prepared for reflected light microscopy, using a modified method described by Edwards (1968). To prevent the crumbling of the pyritized axes during sectioning, they were embedded in dental plaster of paris, and were sectioned using a small dental saw. These sections were fixed to glass slides with Canada balsam and ground by hand in the usual way.

The photographs on Pl. 25, figs. 5, 6; Pl. 26, figs. 5, 7, 8; Pl. 27, figs. 3, 5, 6, 7, 9, and Pl. 28, figs. 2, 3, 8, 9 were taken with the Zeiss Photomicroscope III Stand, and the micrographs on Pl. 25, fig. 3; Pl. 27, figs. 1, 2, 4; and Pl. 25, fig. 4 with the Cambridge S 600 SEM in the Department of Botany, Birkbeck College, University of London.

The remaining photographs were taken with an Exakta camera and a Zeiss-Jena lightmicroscope in the Botanical Institute of the Jagiellonian University, Kraków.

SYSTEMATIC PALAEONTOLOGY

Order ZOSTEROPHYLLALES
 Family ZOSTEROPHYLLACEAE
 Genus KONIORIA gen. nov.

Konioria andrychoviensis sp. nov.

Plant fragments extracted from the rock samples include axes with both long and short spines, axes with only short or long spines, sterile and fertile apices, and pyritized axes (Table 1).

TABLE 1. Characters found on separate parts of the plant which indicate that they belong to the same plant (cross indicates presence of character)

PLANT PARTS CHARACTERS	Axis with long and short spines	Axis with long spines only	Axis with short spines only	Sterile apex	Fertile apex	Pyritised axis	Circinately coiled axis
Long spines with minute teeth	+	+	-	-	-	+	+
Short spines	+	-	+	+	+	+	+
Wing	+	+	+	+	+	+	-
Stomata	-	-	+	+	+	-	-

Axes with spines. The *Konioria* axes are preserved on the bedding planes in a dark-grey siltstone. The core is 9 cm wide which limits the length of the specimens; originally they were longer. There are also many pieces which were broken into short lengths before deposition.

The axes dichotomize into unequal or almost equal parts diverging at about 30° (Pl. 25, figs. 1, 4). The distance between successive dichotomies is about 4 cm towards the top of the plant. Below dichotomies the axes widen and gradually change into two branches. One axis was 2 mm wide at 1 cm below its first dichotomy and 1.5 mm at 1 cm below its second dichotomy. The length of this axis is over 6 cm. Other specimens suggest a possible length of about 15 cm for the largest axes which are 4 mm wide. The length of the plant is unknown but some estimate is possible by relating the extent of tapering along a single axis to the extremes of axis diameter (0.3–4.0 mm).

The longest unbranched axis available is 7 cm but most branch at closer intervals than this and near the apex branching is very close together. Successive dichotomies are not all in the same place but the precise angle between them in the lower part cannot be given. Near the apex it is about 90°. A characteristic and remarkable feature of the axes is that they have one to four longitudinal wings. These may lie in the plane of compression (Pl. 25, fig. 4) where they appear as borders to the axis, or they may be present on the surface of the axis (Pl. 25, figs. 5,

EXPLANATION OF PLATE 25

Fig. 1. Paratype, axes with two branches, S/98/14; $\times 1.2$.

Fig. 2. Axes with long spines, S/98/12b; $\times 3$.

Fig. 3. SEM. Stem with long and short spines; $\times 120$.

Fig. 4. Axes with 'compression margin' (wings), S/98/9a; $\times 3$.

Fig. 5. Surface of axis showing three wings (arrowed) (specimen destroyed); $\times 126$.

Fig. 6. Compressed axis showing wing and a long spine at an acute angle (specimen destroyed); $\times 6$.



6; Pl. 26, figs. 7, 8; Pl. 27, fig. 6; Pl. 28, figs. 2, 9). These wings are present on tall axes. Occasionally, the wings take a spiral course (Pl. 28, fig. 9) which is not the result of twisting of the axis. Twisted axes are seen on Pl. 25, fig. 6. On wings as well as on the axes, the spines may be dense (Pl. 26, fig. 6). The author considered the possibility that the wings were mere compression borders, but decided they were not, on the evidence given below:

1. In transverse sections of pyritized axes the wing is continuous with the thick, carbonized layer (Pl. 26, fig. 6).
2. Cells of the hypodermal layer below the carbonized layer do not enter the wing (Pl. 26, fig. 6).
3. In a transverse section of a flattened pyritized axis the wing is not a continuation of the longer axis of the section. If the wing were formed as a result of flattening of the plant, it would occur in the same plane (Pl. 26, fig. 6).
4. Often the wing forms a spiral on the axis (Pl. 28, fig. 9).

Axes bear spines of varying size and frequency. The spines range from being short and triangular to long and subulate (Pl. 25, fig. 3). On the rock the spines are visible at the sides of the axes, while on their surface only their bases are seen as large and small dots. The spines are distributed irregularly; rarely are they very frequent on one surface of the axis and not on the other (Pl. 26, figs. 1, 2). The length of the spines is very unequal on different parts of the axis and range from 0.1 to 4 mm. The longest spines, up to 4 mm long and 0.3 mm wide at the base are on the thickest axes, but occasionally there may be fairly long spines on the narrower axes (Pl. 26, fig. 3), and occasionally just one long spine is present (Pl. 28, fig. 3). Usually the narrower axes bear shorter spines (Pl. 26, fig. 5; text-fig. 1) or occasionally none at all. On some axes (Pl. 26, fig. 2) both long and short spines occur. Most spines are at about 90° to the axis. The longer spines show longitudinal ridges (Pl. 27, fig. 2) with occasional minute teeth 12–16 µm long (Pl. 27, figs. 2, 4). Teeth are not obvious on the shorter spines (Pl. 25, fig. 3). The long spines with teeth are most numerous on some circinately coiled axes (Pl. 28, fig. 8) which the author thinks possibly represent early stages in the development of a shoot (these are not included in the reconstruction). Some spines show a dark core of unknown cellular structure (Pl. 28, fig. 3) suggesting a vascular strand. Such structures are spines and not sporangial stalks, because they are quite long and situated at the side of the axis and not below the dichotomies.

Cuticle preparations of axis showed no clearly marked epidermal cells (Pl. 25, fig. 3) apart from dark stomata. The stomata are visible as irregularly distributed elliptical dark dots, because they are usually covered with a dark substance (Pl. 28, figs. 1, 7). They are oval and orientated longitudinally, and sometimes show the guard cells. The spines have no stomata.

Apex of axis. All apices whether sterile or fertile are much branched and curved to form hooks (text-fig. 1; Pl. 26, fig. 5; Pl. 27, fig. 6; Pl. 28, figs. 1, 2). These illustrations show all the variation observed in both sterile and fertile apices. The spines on the ends of axes are never long, and are sometimes infrequent or absent (text-fig. 1). The vascular strand may be visible by scanning electron microscopy but not after maceration. The dark strand in Pl. 28, figs. 1, 7, shows an untreated specimen photographed by transmitted light.

Fertile axes. The sporangia cannot be distinguished on axes still in the rock, probably because the diameter of a sporangium is not much larger than the width of the axis below the dichotomy. They are visible only on axes removed with hydrofluoric acid. Most of the distal branches are sterile, but in some instances a single sporangium occurs at the final or penultimate dichotomy, and perhaps also further down. The sporangia are mostly situated slightly below the angle of the dichotomy and any stalk they possess must be very short and is concealed (Pl. 26, figs. 7, 8; Pl. 28, fig. 2; text-figs. 2, 3). It appears that the small mound visible on the surface of most sporangia is

EXPLANATION OF PLATE 26

Figs. 1, 2. Two sides of a pyritized axis, S/98/23; $\times 17.5$. 1, surface with numerous short spines. 2, surface with bases of two long spines and a few short spines.

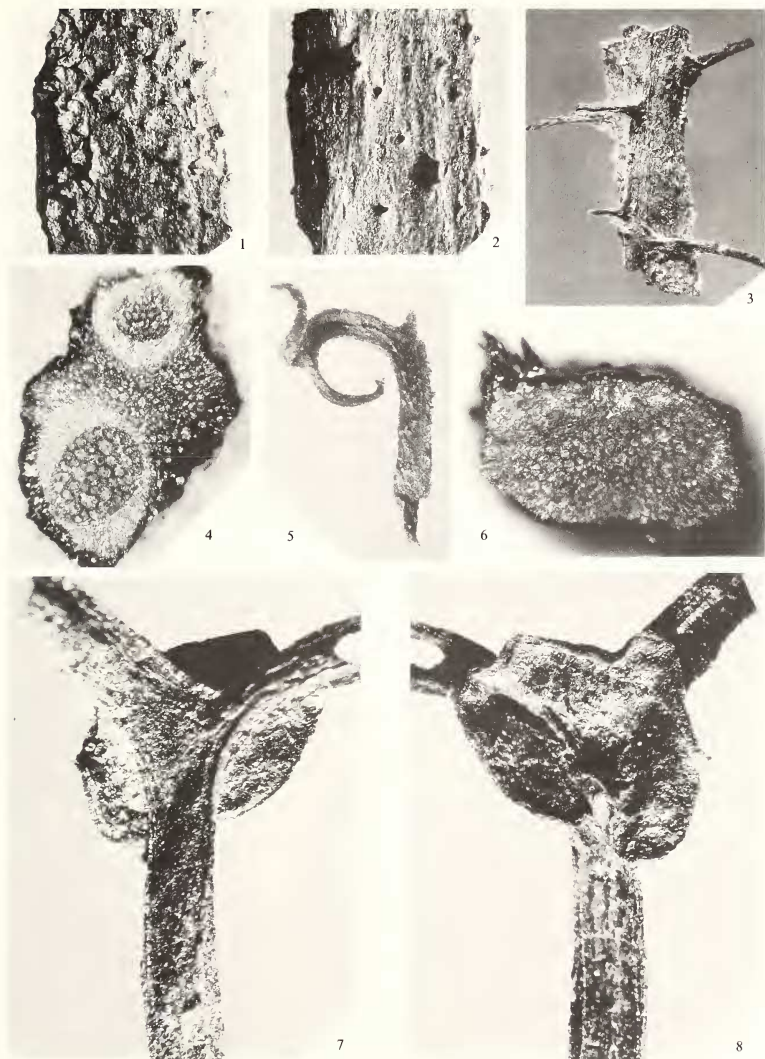
Fig. 3. Fragment of axis with long spines and wing, S/98/26; $\times 20$.

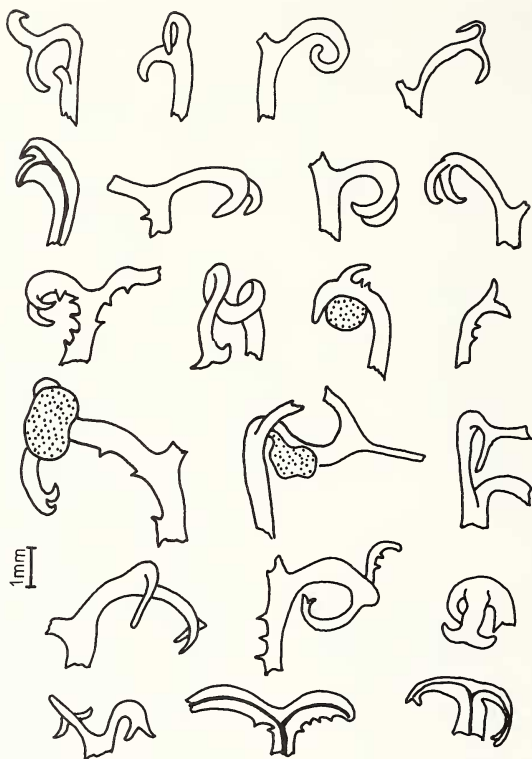
Fig. 4. Pyritized axis just below dichotomy (specimen destroyed); $\times 30$.

Fig. 5. Apex showing short spines, S/98/26; $\times 20$.

Fig. 6. Transverse section of pyritized axes. On the left-hand side is a wing with spines, S/98/79; $\times 25$.

Figs. 7, 8. Holotype, fragment of axis with sporangium situated at the level of a dichotomy (both sides), S/98/31; $\times 30$.

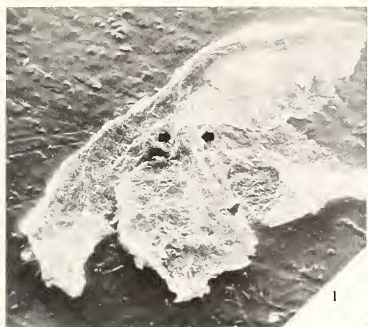




TEXT-FIG. 1. The variation in sterile and fertile hook apices, S/98/37-40.

EXPLANATION OF PLATE 27

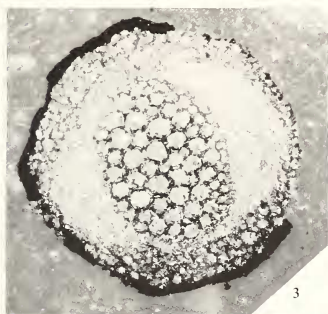
- Fig. 1. SEM. Axis with two flattened branches and a stalked sporangium (arrows); $\times 30$.
 Fig. 2. SEM. Surface of spine showing longitudinal ridges with minute teeth; $\times 300$.
 Fig. 3. Paratype, transverse section of uncompressed axis showing elliptical xylem strand, S/98/15; $\times 50$.
 Fig. 4. SEM. Long spine with round base and minute teeth; $\times 25$.
 Fig. 5. Cells of hypodermis in longitudinal section, S/98/18; $\times 125$.
 Fig. 6. Forked apex showing wing on under side (specimen destroyed); $\times 20$.
 Fig. 7. Protoxylem and metaxylem in longitudinal section showing scalariform tracheids, S/98/17; $\times 110$.
 Fig. 8. Pyritized axis split longitudinally and showing vascular strand with circular bordered pits, S/98/49; $\times 375$.
 Fig. 9. Metaxylem and protoxylem from fig. 3; $\times 167$.



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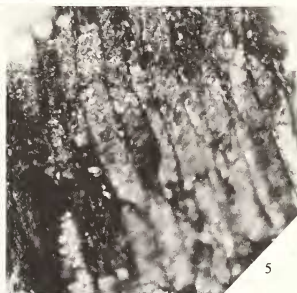
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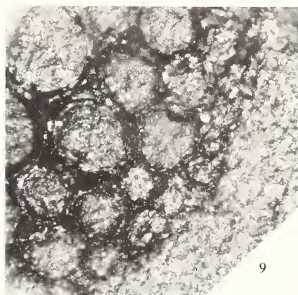
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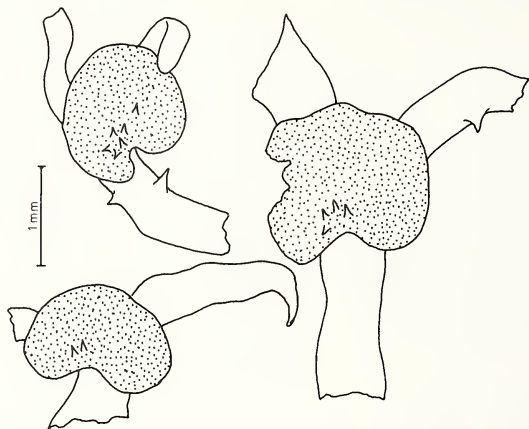


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caused by the stalk (Pl. 26, fig. 8). Some, however, have a longer stalk which is clearly inserted in the angle of the dichotomy (Pl. 27, fig. 1).

The sporangia are flattened and composed of two equal valves which separate along their entire margin. The largest are oval or slightly reniform (Pl. 26, figs. 7, 8; text-fig. 2) but some are round (Pl. 28, fig. 2; text-fig. 2). They are typically about 2.5 mm wide, but the round ones are smaller and one was only 0.5 mm wide. The surface of the outer valve may show diverging cells under scanning electron microscopy. Often the surface of a sporangium bears minute spines (text-fig. 2). Nothing is known of the deeper layers of the sporangial wall. Along the line of dehiscence the wall is flat and appears thin (Pl. 28, fig. 4). Although the two valves are always pressed together the sporangia seem to have dehisced and shed all their spores. Maceration yielded no spores nor did it yield a central mass which might represent compacted spores.

Pyritized axes. Ten pyritized axes were studied. They are rather narrow, 0.5–2 mm wide. Some show long spines (Pl. 26, fig. 3), some short spines and long broken spines (Pl. 26, fig. 2), and some all short spines (Pl. 26, fig. 1). These specimens were not sectioned, the sections being prepared from unfigured specimens which did show short spines or bases of long spines.



TEXT-FIG. 2. Sporangia attached below the dichotomy. Small spines present on the surfaces of sporangia.

EXPLANATION OF PLATE 28

- Fig. 1. Paratype, naturally cleared apex showing dark core and stomata as dark spots, S/98/29; $\times 25$.
 Fig. 2. Apex with sporangium (specimen destroyed); $\times 30$.
 Fig. 3. Fragment of axis with spines; large spine apparently with ?vascular strand coming from the axis, S/98/27; $\times 20$.
 Fig. 4. SEM. Fragment of sporangium valve; margin appears to be thin and smooth, but the wall shows ?papillae; $\times 300$.
 Fig. 5, 6. Tracheids isolated by Schulze maceration from carbonized axis. Tracheids show circular bordered pits. 5, S/98/75; $\times 600$; 6, S/98/76; $\times 546$.
 Fig. 7. Naturally cleared apices showing stomata as dark spots on the epidermis, S/98/30; $\times 24$.
 Fig. 8. Young coiled axis densely covered with long spines, S/98/25; $\times 20$.
 Fig. 9. One branch of the dichotomy (the other broken off) showing spiral wing (specimen destroyed); $\times 19.5$.



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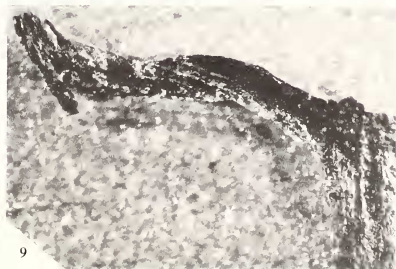
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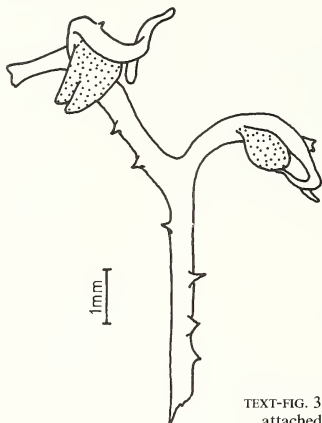


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The transverse section on Pl. 27, fig. 3, shows a black, coalified outer layer which can be regarded as the epidermis, inside this are about four layers of thick-walled cells which represent the hypodermis. Occasionally the outer coalified layer is thicker, suggesting that the hypodermal cells are also coalified. In longitudinal section the hypodermal cells are elongated and show no obvious pits (Pl. 27, fig. 5). Length of cells from 150 to 450 μm , width from 30 to 85 μm .



TEXT-FIG. 3. Paratype, axis with two sporangia attached below the dichotomies, S/98/35.

Inside the hypodermis, there is a region in which the cells are scarcely visible, and these surround a circular (Pl. 26, fig. 4) or elliptical (Pl. 27, fig. 3) xylem strand, with small tracheids (regarded as protoxylem) to the outside and larger tracheids (regarded as metaxylem) to the inside (Pl. 27, fig. 9). The metaxylem shows well-developed scalariform tracheids (Pl. 27, fig. 7). Three different stems showed exactly similar scalariform tracheids with no round pits. However, a further specimen with the surface fractured longitudinally showed round pits in what appears to be a metaxylem tracheid (Pl. 27, fig. 8), but when this stem was polished, no pits were seen. The author believes that the round pits do not represent pyrite crystals, which usually have an angular outline. Yet another specimen (showing small spines), which was not pyritized, was unusual when macerated in Schulze's solution, in that it yielded excellent tracheids in longitudinal view, which showed round bordered pits in two rows in some of the tracheids (Pl. 28, figs. 5, 6). The variety of xylem pitting is large, but such evidence does suggest that all the specimens belong to one species.

Reconstruction of Konioria

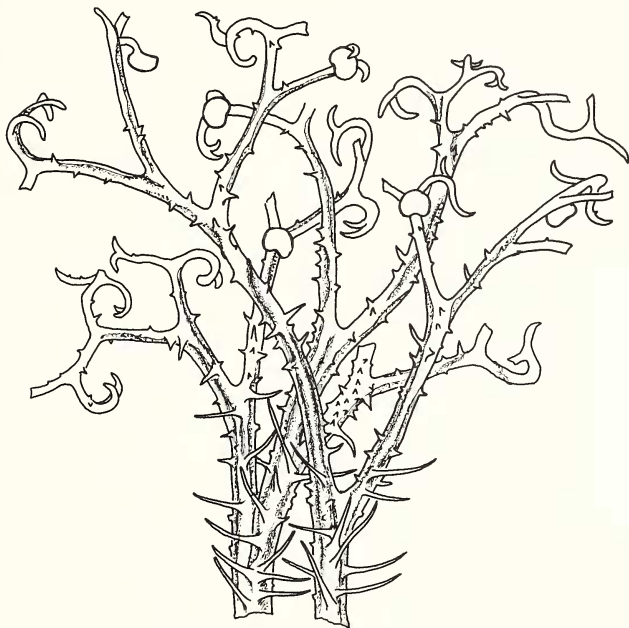
There are no large specimens of this plant available, but the separate fragments are linked by common characters (Table 1). The reconstruction (text-fig. 4) is made from the drawings of all those separate parts.

Konioria gen. nov.

Type species. Konioria andrychoviensis sp. nov.

Diagnosis. Erect axes slender, branching by more or less equal dichotomy in different planes. Lower dichotomies further apart than upper ones. Apices narrow to points, and are curved to form hooks. Axis usually with 1–4 narrow longitudinal wings. Surface of axes with spines, which range from long and subulate to short and triangular. Epidermis of axis with longitudinally orientated stomata. Inside the epidermis is a hypodermis of up to four layers of thick-walled cells. The hypodermal cells are rounded in transverse section but elongated longitudinally. The area of the cortex and phloem, is not

preserved. A central xylem strand has the smallest tracheids to the outside. Metaxylem tracheids have scalariform thickening. Sporangia are borne singly below dichotomies, usually on short stalks. The sporangia are round or reniform in outline, and composed of two equal valves, with the dehiscence line along the whole margin.



TEXT-FIG. 4. Reconstruction of *Konioria andrychoviensis*, $\times 3$ (approx.).

Konioria andrychoviensis sp. nov.

Plates 25–28

1965 *Psilophyton* sp. Reymanówna in Konior, p. 217, figs. 1, 3.

Diagnosis. Axes 0.3–4 mm wide, branching frequently, with short to long spines. Lower part of axis bearing subulate spines up to 4 mm long usually with minute lateral teeth, the upper part of the axis has shorter and triangular spines. Sporangia up to 2.5 mm wide but often smaller, frequently bearing minute spines near their bases.

Horizon. Lower Devonian, Emsian.

Locality. Two bore-holes Andrychów 2 and Andrychów 4 in the Bielsko–Andrychów area of the Western Carpathians, Poland.

Type specimens. All specimens are deposited in the Palaeobotanical Museum of Institute of Botany, Jagiellonian University, Kraków, S/98. Holotype: S/98/31, Pl. 26, figs. 7, 8. Paratypes: S/98/4, Pl. 25, fig. 1; S/98/35, text-fig. 4; S/98/15, Pl. 27, fig. 3; S/98/29, Pl. 28, fig. 1.

Derivation of name. The generic name *Konioria* is after Professor Konrad Konior who found the material and was kind enough to give it to the author for investigation. The specific name is derived from the name of the locality Andrychów.

DISCUSSION

Comparison with Psilophyton goldschmidtii and P. arcticum

Konioria might be confused with *P. goldschmidtii* (Halle 1916) and *P. arcticum* (Høeg 1942), because of similar external morphology of the axes as seen when on the rock surface. A character common to both *Konioria* and *P. goldschmidtii* is the 'compression margin' (wing), which is distinctly visible on specimens seen on the rock surface. Halle (1916) gives no explanation of its nature. In *Konioria* the 'margins' are in fact wings running along both sides of the axis. A second similar character are the subulate spines of variable length up to 4 mm. The spines of *P. goldschmidtii*, however, are less numerous. The two plants differ in their branching. In *Konioria* the axes dichotomize, whilst in *P. goldschmidtii* the branching is sympodial and dichotomous. The axes of *Konioria* are straight while in *P. goldschmidtii* they are zigzag shaped (Nathorst 1913; Halle 1916; Høeg 1967). In *P. goldschmidtii* the anatomical structure of the axes and the sporangia are unknown. Although these two plants show several common characters, the differences between them and the different mode of preservation suggest that the new plant should not be included in *P. goldschmidtii*. When comparing these two plants, the author was able to study the figured specimen described by Halle (1916). The similarities and differences between the two plants mentioned above were confirmed by this material.

In 1959 Ananiev described *P. goldschmidtii* from the Devonian of south-eastern Siberia. Ananiev gives no description of the plant, but his photographs (Pl. 7, figs. 1, 2, 4; Pl. 8, fig. 4; Pl. 12, fig. 1; Pl. 14, figs. 1, 2; Pl. 24, fig. 2a) clearly show the differences between the branching of *Konioria* and *P. goldschmidtii*.

In 1932 Lang described *P. princeps* and *P. goldschmidtii* from the Strathmore Beds in Scotland under the name *Psilophyton*. The *Psilophyton* figured by Lang on Pl. 2, figs. 24, 25, 27, is similar to *Konioria* in that it shows axes with a 'compression margin' (wing). His Pl. 2, figs. 24, 33, shows the presence of short spines and bases of broken long spines similar to *Konioria*. The differences in branching between the two plants are clearly seen when comparing Lang's Pl. 2, figs. 24, 25, 27, with *Konioria*. Lang describes the branching as pseudomonopodial, which is clearly different from the dichotomous branching in *Konioria*. An investigation of Lang's material in the British Museum of Natural History in London, confirms the similarities and differences between the two taxa.

Konioria shows some external similarity to *P. arcticum* Høeg 1942, which also possesses a distinct margin (see his Pl. 9, fig. 3; Pl. 12, fig. 1). Høeg does not explain the nature of this margin. Unlike *Konioria*, however, *P. arcticum* has pseudomonopodial branching and hair-like spines from 4 to 6 mm long.

Comparison with genera of the subdivision Zosterophyllophytina

Attributing *Konioria* to the Zosterophyllophytina, the author uses the classification of the 'psilophytes' given by Banks (1968, 1975). *Konioria* shows the characters of the subdivision Zosterophyllophytina, i.e. the lateral arrangement of sporangia and the exarch xylem strand.

Comparison with Crenaticaulis and Gosslingia. *Konioria* possesses a greater number of characters in common with *Crenaticaulis* (Banks and Davis 1969) and *Gosslingia* (Edwards and Banks 1965; Edwards 1970) than with other genera. All three plants show dichotomous branching, although *Crenaticaulis* and *Gosslingia* also have pseudomonopodial branching. *Crenaticaulis* and *Gosslingia* also show scars below dichotomies. In *Crenaticaulis* axillary branches are present which were compared by Banks and Davis (1969) with the rhizophores of *Selaginella*. Also, in *Konioria*, the sporangia are borne in the same position. Another character in common in these three genera is that the sporangia do not form spikes.

Konioria differs from *Gosslingia* in possessing spines. *Crenaticaulis* shows characteristic short tooth-like spines arranged in one or two rows, while *Konioria* has irregularly arranged spines ranging from long and subulate to short and triangular. The sporangia of *Gosslingia* and *Konioria* split into two equal valves whilst in *Crenaticaulis* there is a large abaxial and a small adaxial valve.

Comparison with Sawdonia and Euthursophyton. *Konioria* shows a certain similarity with *Sawdonia ornata* (Dawson) Hueber, see for example, Dawson 1871; Hueber 1964, 1971; Hueber and Banks 1967; Ananiev and Stepanov 1968. The two plants have the same dichotomous mode of branching and the lateral arrangement of sporangia which split into two equal valves. *Sawdonia* differs from *Konioria* in having glandular spines and sporangia distributed along the axis.

Konioria and *Euthursophyton hamperbachense* Mustafa (Mustafa 1978) are similar in their dichotomously branching axes covered with long spines, in occasionally showing circinate coiled axes and in possessing an exarch strand. In *Euthursophyton*, however, the sporangia are unknown. *Konioria*, unlike *Euthursophyton*, possesses differentiated spines, from long and subulate with minute teeth to short and triangular. In addition, wings on the surface of the axes are present in *Konioria* but absent in *Euthursophyton*. In the *Euthursophyton* axes no hypodermis has been described.

Comparison with Zosterophyllum and Rebuchia. *Konioria* differs from both *Zosterophyllum* (Croft and Lang 1942; Edwards 1969a, b; Lele and Walton 1961) and *Rebuchia* (Dorf 1933; Hueber 1970, 1972a, b) in not having the sporangia arranged in spikes. In addition, these two genera have smooth axes, which in *Zosterophyllum* show in their lower parts H-shaped branching. Common to *Zosterophyllum*, *Rebuchia*, and *Konioria* are lateral, reniform sporangia splitting into two equal valves. Edwards (1969) demonstrated exarch xylem in *Zosterophyllum llanoveranum*. In *Rebuchia* the xylem strand is not well known, and is mentioned only by Lepekhina, Petrosian, and Radchenko (1962). It is possible that this is also a common character of all three genera.

The systematic position of Konioria

The author accepts the classification of the early land plants into Rhyniophytina, Trimerophytina, and Zosterophyllophytina (see Banks 1968, 1975). The lateral position of sporangia and the exarch xylem strand of *Konioria* suggest its affinity with genera of the subdivision Zosterophyllophytina. Comparisons show that *Konioria* differs from other Zosterophyllophytina in having sporangia attached below a dichotomy, in showing wings on the axis, and in possessing spines ranging from long and subulate to short and triangular. These are the characters of the new genus and species *Konioria andrychoviensis*.

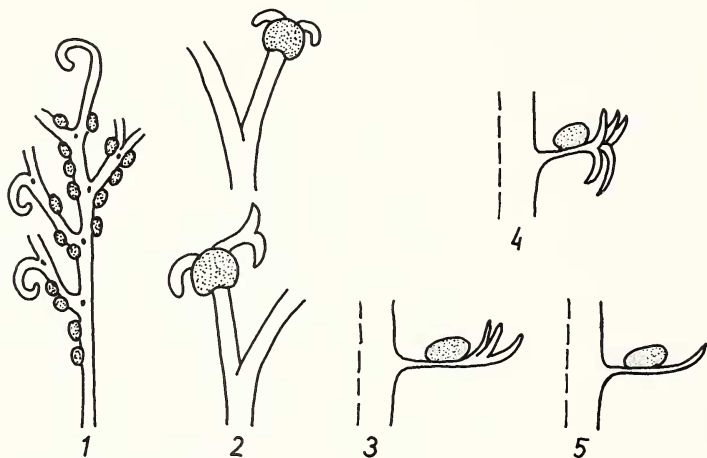
In his classification, Banks (1968) divided the order Zosterophyllales into two families, Zosterophyllaceae and Gosslingiaceae, which differ in the grouping of sporangia. In a later paper Banks (1975) distinguishes only one family, the Zosterophyllaceae. If this later publication were followed, *Konioria* would become a member of the Zosterophyllaceae, fitting well the diagnosis of this family. However, it would appear that a return to the former division of the Zosterophyllophytina into two families would be better, with the Zosterophyllaceae having sporangia in spikes, and the Gosslingiaceae having sporangia scattered along the axis. These two families were also recognized by Kasper, Andrews, and Forbes (1974). Perhaps *Konioria* would even merit the establishing of a third family, characterized by having sporangia attached below the dichotomies.

The morphology and the anatomical structure of *Konioria* provide additional data to support Banks's (1968) classification of the early land plants, in that the morphological characters discussed above are further evidence that the Zosterophyllophytina forms a natural group. This group, according to the hypothesis of Banks (1968; Chaloner and Sheerin 1979), gave rise to the Lycophytina.

Konioria and the evolution of the lycopod sporophyll

The unusual position of the sporangium of *Konioria* appears to be related to that in certain early lycopods. According to Zimmermann (1930) the sporophylls of the lycopods developed from

ultimate branchlets with sporangia of the *Rhynia*-type. However, according to Banks (1968), the Rhyniophytina gave rise to all groups of plants, except the lycopods which developed from the Zosterophyllophytina. This opinion is confirmed by the anatomical structure and the type and arrangement of sporangia in the Zosterophyllophytina. Accordingly, the intermediate forms leading to the sporophyll of lycopods have been looked for among the Zosterophyllophytina. In accordance with Zimmermann's Telome Theory, the processes of *Konioria* suggest an evolutionary sequence of the lycopod sporophyll from the Zosterophyllophytina. Text-fig. 5 is an attempt to arrange such a



TEXT-FIG. 5. Proposed evolutionary sequence of the lycopod sporophyll. 1, *Gosslingia*; 2, *Konioria*; 3, *Colpodexylon*; 4, *Leclercqia*; 5, *Cyclostigma*.

sequence of existing fossil plants, which could lead to the sporophylls of lycopods. The starting-point is *Gosslingia* (Edwards 1970), which bears lateral sporangia scattered along the axis. The next stage is *Konioria* with lateral sporangia borne below dichotomies. Therefore, *Konioria* would appear to be the link between the Zosterophyllophytina and such lycopods as *Colpodexylon* (Banks 1944) and *Leclercqia* (Banks, Bonamo, and Grierson 1972) which have a sporophyll divided into three or more segments. The unequally dichotomizing axes of *Konioria* can be regarded as the initial form from which the sporophylls of those lycopods originated. It can be assumed that the wider branch of the unequal dichotomy of *Konioria* would change into the main axis, as a result of the process of overtopping. The other narrower branch of *Konioria* consisting of ends of axes with a sporangium attached at the basis of the dichotomy, could be transformed into the lycopod sporophyll by the processes of planation and reduction. In *Konioria* there are unequal dichotomies of the hook-like apices under which the sporangia are attached. Therefore, it is possible to derive the sporophylls of *Colpodexylon* directly from *Konioria*, because in *Konioria* there are apices with three or four branches above the sporangium. It is more difficult to derive the sporophyll of the lycopod *Leclercqia complexa*, which ends with five segments, from *Konioria*, because five times divided apices of *Konioria* were not found. In theory, however, such branching is also possible.

There is also the theoretical possibility of deriving the undivided sporophylls of *Cyclostigma* (Chaloner 1968) and similar lycopods by a reduction from sporophylls showing more than one division.

As a result of those considerations, the explanation by Zimmermann (1930) of the origin of the lycopod sporophyll from sterile and fertile axes by overtopping and reduction appears justified, and can be envisaged directly from the Zosterophyllophytina, but not from the Rhyniophytina. The sequence proposed in the present paper appears to confirm the axial origin of the lycopod sporophyll.

In the light of new facts established about the position of sporangia in *Drepanophycus* and *Protolopododendron*, these two genera are excluded from the sequence. *Drepanophycus* (*Protolycopodites*) *devonicus* is not placed here, because Schweitzer and Giesen (1980) established that sporangia of this plant do not occur on sporophylls, but on the axis among microphylls. According to Schweitzer and Giesen, the sporangia in *D. spinaeformis* Goepp. also have a similar position, and do not occur on the sporophyll as described by Kräusel and Weyland (1930). Also, *Protolopododendron scharianum* Potonié and Bernard which according to Kräusel and Weyland (1932) possessed bifurcating sporophylls is not shown in the sequence. According to Schweitzer and Giesen (1980), its sporophylls show a double dichotomy with a sporangium present below each dichotomy. Schweitzer and Giesen think that *P. wahnbachense* Kräusel and Weyland also shows this type of sporophyll (see their reconstruction (text-fig. 12, p. 15)). However, there exists a controversy about this reconstruction, because according to Fairon-Demaret (1979) these sporophylls bear several sporangia, and she tentatively attributes this plant to the Sphenopsida and not to the Lycopsidea.

In summary, the above considerations demonstrate the possibility that the lycopod sporophyll may have originated through a change in the ends of axes into sporophylls divided into segments, and to a reduction of the number of these segments (text-fig. 5).

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